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STUDIES ON THE INHERITANCE OF SMUT REACTION,
LEMMA COLOR, AWN DEVELOPMENT AND
RACHILLA PUBESCENCE IN OATS.

L.P.V. Johnson

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University of Alberta

April, 1933.

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The undersigned hereby certify that they have read and recommended to the Committee on Graduate Studies for acceptance a thesis on "Studies on the inheritance of smut reaction, lemma color, awn development and rachilla pubescence in oats," submitted by L.P.V. Johnson, B.Sc., in partial fulfillment of the requirements for the degree of Master of Science.

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L.P.V. Johnson
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A THESIS
submitted to the University of Alberta
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TABLE OF CONTENTS.

	<u>Page..</u>
Introduction	1
Materials and Experimental Methods	3
Parental material	3
Inoculum and methods of inoculation	4
General methods of growing and handling the material	5
Environmental considerations	7
Inheritance of Smut Reaction	9
Historical review	9
Experimental results	14
Inheritance of Lemma Color	20
Historical review	20
Experimental results	21
Inheritance of Awn Development	25
Historical review	25
Experimental results	26
Inheritance of Rachilla Pubescence	33
Historical review	33
Experimental results	33
Studies on Correlated Inheritance	39
Correlations between smut reaction and other characters.....	39
Correlations between various grain characters	44

Table of Contents (Continued).

	<u>Page.</u>
Economic Significance	46
Summary	47
Acknowledgement	49
Literature Cited	50
Appendix	53

STUDIES ON THE INHERITANCE OF SMUT REACTION,
LEMMA COLOR, AWN DEVELOPMENT AND
RACHILLA PUBESCENCE IN OATS.

L.P.V. Johnson.

INTRODUCTION

The control of oat smuts is of great economic importance because of the wide distribution and destructiveness of these diseases. Canadian farmers suffer a yearly loss of nearly seven million dollars from oat smut (14).

In Alberta, covered smut, caused by *Ustilago levis* (K. and S.) Magn., is very common while loose smut caused by *Ustilago avenae* (^P*vers.*) Jens. is relatively rare (4,5). In 1930, covered smut damage in Alberta fields ranged from zero to thirty-five per cent; absence of the disease was apparently due to proper seed treatment (5). In 1931 nearly one-half of the fields ^{examined} were infected by covered smut (4).

Chemical and other seed treatments are usually quite efficient in controlling oat smuts; but, as such methods are troublesome and add to the cost of production, it would appear that a more desirable means of preventing smut infection would be the breeding and use of smut resistant oat varieties. The present investigation is mainly a

study of the reaction to covered smut of progeny of crosses between the standard commercial varieties, Victory and Banner, and a smut resistant variety of inferior quality, Black Mesdag, the object being to obtain constant strains possessing the desirable characters of both parents, and to record genetic data on the reaction to the disease. Genetic data were also compiled on lemma color, awn development, and rachilla pubescence for the purpose, in each case, of studying the mode of inheritance of the character and of testing its relation to smut reaction and to the other characters studied.

MATERIALS AND EXPERIMENTAL METHODS.

Parental material

The cultures used in these studies were F_1 to F_3 generations (complete) and certain F_4 lines of the crosses Black Mesdag x Victory and Black Mesdag x Banner. A comparison of these varieties for the characters studied is summarized in Table I.

Table 1.

Comparison of parental varieties
for characters studied.

Variety	Lemma color	Awn development	Rachilla pubescence	Callus pubescence	Av. percent age infec- tion by covered	smut
Victory	white	usually weak; often slightly twisted, seldom geniculate	absent	Occasional- ly a few short hairs		89.2
Banner	white	weak to medium strong; usual- ly twisted, occasionally geniculate	absent	ditto.		84.5
Black Mesdag C.I.1877	black	strong; twist- ed, geniculate	numerous hairs present	ditto.		0.0

Victory and Banner differ slightly for the character of awn development, Banner having a somewhat stronger expression; but for the characters of smut reaction, lemma color, rachilla pubescence and callus pubescence the two varieties are practically identical. Comparing Black Mesdag with Victory and Banner shows that in lemma color and smut reaction the parents are entirely different, the former is black and immune, the latter are white and susceptible. Black Mesdag has a far stronger development of awns, it has fairly heavy rachilla pubescence which contrasts the glabrous condition of the other parents. All three varieties are practically the same with respect to callus pubescence.

Inoculum and methods of inoculation.

Only the ^{reaction to} covered smut of oats, caused by Ustilago levis (K. and S.) Magn., was ^{studied} used in the present test. In 1930 a composite was made up of smutted panicles collected from many different varieties in many parts of the province. Inoculum was prepared by grinding the infected panicles of this collection. In 1931 several field smut tests were carried on which included some 250 varieties and about 450 hybrid lines including 165 F_3 lines of the present material. Smutted panicles were collected from over 200 varieties and from nearly 300 hybrid lines. The composite ^{spore material obtained} ~~made~~ from this collection served as inoculum for the retesting, in 1932, of the F_3 lines of the present study.

Reed (23, 25, 27) and Reed and Stanton (30) have reported evidence indicating the existence of several physiologic races of both oat smuts^{fungi}. It is believed that the inoculum used in the present investigation includes the majority, if not all, of the physiologic forms of ^{the} covered smut^{fungi} existent in the province.

As the 1931 smut test of F_3 lines, in which hulled seeds (hulls not removed from caryopses) were used, resulted in only fair smut infection, it was decided to repeat the test in 1932 using dehulled seeds (hulls removed from caryopses). Fifty seeds, or as many as available up to that number, of each F_2 plant were dehulled and placed in an envelope. The inoculum was prepared by grinding the smutted panicles and removing the chaffy material by sifting. A liberal quantity of inoculum was added to each envelope which was then shaken vigorously. The smut infection in 1932 was very severe. Previous investigators, particularly Johnston (17) and Stanton et.al. (32), have found dehulling of the seed to greatly increase smut infection.

General methods of growing and handling
the material.

In all, three complete sowings were made from F_2 seeds: in 1931 duplicate sowings were made, one being a genetic nursery used as a source of material for morphological studies, the other being a smut test; in 1932 the smut

test was repeated. In all sowings, plots of both parents were grown between every 20 hybrid plots. All plots were single rows, ten feet in length, with 50 seeds (or as many as available) per row.

Notes on smut infection were taken in the field when plants neared maturity, infection then being complete. Counts of total number of plants and of number of plants infected were made in each hybrid and parental row. (Plants were spaced approximately two and one-half inches apart to facilitate counting.) From data thus collected the percentage of smut infection was later calculated for each row.

Field notes were also taken on early growth habit, date of heading, date of maturity and on leaf area infected with halo blight disease. A study of these data is not included in the present paper.

The plants in the genetic nursery plots were harvested by pulling up each plant by the roots, and making a sheaf from each line. The data on awn development were compiled for each plant prior to threshing. Data on all other morphological characters were compiled from threshed seed. It should be stated that in threshing the outer glumes of many spikelets were not removed. Seeds thus protected were utilized to advantage in classifying for pubescence, as completely threshed grains often lost many hairs in the process.

Environmental considerations

Bartholomew and Jones (2) found that the temperature optima for growth, spore germination, and sporidial production in Ustilago avenae were 68°, 59°, and 59° F. respectively. In soil of 36 percent moisture, 100 percent infection was obtained at temperatures between 59° and 73° F. Reed and Faris (28) obtained highest infections by U. levis at 77° F. with severe infections at 59° and 68° F. Johnston (17) found soil temperatures of 62° to 66° F. to be the most favorable for infection by a mixture of U. avenae and U. levis.

In the spring of 1932 observations were made on soil temperatures by means of a thermograph. Seeding was done on May 6th when soil temperatures ranged from 52° to 65° F. with the average at 59° F. Temperatures for the three days preceding had been practically the same, and there was little change in average soil temperatures up to the time of emergence of the seedlings. It is believed that the temperature conditions of the present experiment were near to optimum for smut infection.

The Oat Smuts.



Ustilago levis (Covered smut) Ustilago avenae (Wheat smut)

Plate 1.

The Oat Smuts

INHERITANCE OF SMUT REACTION.

Historical review.

Literature on the inheritance of smut reaction in oats is comparatively recent. It dates from 1920 when Wakabayashi (34) published data on the behavior of the progeny of a cross, Red Rustproof x Black Tartarian, to Ustilago levis. Red Rustproof is resistant, Black Tartarian susceptible. In the F_3 , twelve families out of a total of 107 showed a few smutted plants. He concluded that immunity was dominant and perhaps due to three independent factors.

Barney (1) reported on the reaction of the progeny of three crosses to U. avenae. One cross, Fulghum x Black Mesdag, involved two highly resistant varieties; a second cross, Swedish Select x Burt involved a highly susceptible and a resistant variety, respectively; a third cross, Turkish Rustproof x Gold Rain involved a highly susceptible and a moderately susceptible variety, respectively. Barney concluded that in the first cross resistance depended upon three independent factors, in the second upon two, and in the third upon one.

Reed and Stanton (29) published on the reaction of selections from a cross, Fulghum x Swedish Select, to both U. avenae and U. levis. Fulghum is highly resistant to both smuts, while Swedish Select is susceptible to

both smuts. Evidence was presented which indicated that resistance to both forms was dependent upon the same genetic factors. The reaction of 93 F_3 families was studied; 25 were as resistant as the Fulghum parent, eight were more susceptible than the Swedish Select parent, the remaining 59 showed moderate to high susceptibility. The F_4 selections from susceptible F_3 families all showed high susceptibility. With two exceptions, F_4 selections from resistant F_3 families proved very resistant. No correlation between smut reaction and morphological characters was observed. They concluded, therefore, that it is possible to obtain the desired combination of smut resistance and other varietal characters in oats.

Reed (24) studied the inheritance of loose smut reaction in a cross Avena nuda var. inermis (susceptible) x A. sativa var. Black Mesdag (resistant). Results indicated that resistance to U. avenae is dominant while susceptibility is recessive, and that there is a single factor difference between the parents. No correlation between smut reaction and morphological characters was observed.

Gains^c (10) published data on the reaction of oat varieties and hybrids to covered smut. The resistant variety, Red Rustproof, was crossed with four susceptible varieties. Crosses with Black Tartarian and with Abundance indicated that Red Rustproof carries three dominant factors for immunity, any one of which prevents infection by U. levis. In crosses with Large Hulless and with Chinese

— 3 —

the first time I have ever seen a bird of this species. It was a large bird, about 12 inches long, with a very long, thin, slightly curved bill. Its plumage was dark brown, with some lighter feathers on the wings and tail. It had a crest on its head and a long, dark, bushy tail. It was perched on a branch of a tree, looking around at the other birds in the flock. I took a few steps closer to it and it flew away. I followed it for a short distance and then it landed on another branch. I took a few more steps closer and it flew away again. This happened several times, with the bird always flying away and then landing on another branch. Finally, I got close enough to it and it flew away for good. I never saw it again.

Hulless, Red Rustproof was again shown to carry three factors for resistance, but one of the factors did not possess complete dominance in hulless segregates, otherwise the prepotency of the factors were the same in all four crosses.

Hayes, Griffee, Stevenson and Lunden (16) studied the inheritance of reaction to both smut fungi using as cultures 378 selected F_3 lines from the cross (White Russian x Minota)x Black Mesdag. They concluded that immunity is dominant to susceptibility and that there is no correlation between glume color, awn development, number of hairs on rachilla, rust reaction and smut reaction. They found it impossible to state the exact genetic constitution with respect to smut reaction, but state that their results could be explained by assuming two pairs of genetic factors, II and RR, for immunity and resistance, respectively, located in Black Mesdag. I might be considered to be epistatic to R. Several homozygous lines were obtained which were immune to smut, resistant to rust, and which possessed white glumes and weak awns.

Reed (26) studied crosses between varieties susceptible to both smuts and varieties resistant to both smuts; between varieties susceptible to both smuts; between varieties resistant to covered smut but susceptible to loose smut and varieties susceptible to both smuts; between a variety susceptible to both smuts and a variety susceptible to covered smut but resistant to loose smut. He states that "In all the crosses involving varieties differing in their behavior to smut, resistance

was dominant and susceptibility recessive, and segregation in the F_2 appeared to occur on the basis of a single factor difference". In crosses between susceptible varieties, the F_2 descendants were in every case as susceptible as the parent varieties.

Garber, Giddings and Hoover (12) reported studies of the F_3 and F_4 of a cross, Gopher x Black Mesdag, and the reciprocal. Gopher is moderately susceptible, while Black Mesdag is immune to both smuts. They concluded that smut reaction was controlled by a single main factor and at least one supplementary factor, which caused transgressive segregation. There was some evidence of correlation between the supplementary factor and the factor for black lemma color. No correlation existed between smut reaction and the characters, leaf width and earliness.

In a later paper (13) the same authors published further studies on transgressive segregation for susceptibility in the same material. They assume that Black Mesdag is homozygous for a dominant factor R which gives high resistance, possibly immunity, and that Gopher is homozygous for a factor I which is an additional factor for resistance but less potent than R. Black Mesdag carries the recessive factor for susceptibility i, and Gopher the recessive factor for susceptibility r. I may act as an inhibitor to r. Thus Black Mesdag may be genetically represented as RRii, and Gopher as rrII. The genotypes rrIi and rrii segregating from the cross have

potentialities for greater susceptibility than Gopher, and their theoretical frequencies correspond to observed frequencies of families showing transgressive segregation for susceptibility.

Welsh (35) published results of a study on the reaction of F_3 progeny of the cross Victory x (Minota-White Russian x Black Mesdag) to both smuts. The former is resistant and the latter susceptible to both smuts. The same F_3 lines were tested with each form of smut separately. Transgressive segregation occurred. By classing all lines not more susceptible than the Victory parent as resistant, R, and all other lines as susceptible, S, he found that the deviations from the ratio R:S = 15:1 were, for the loose smut test, 3.15 ± 2.83 , for the covered smut test, 10.81 ± 2.83 . He concluded that at least two factors govern smut reaction, and that resistance is dominant. A correlation coefficient of 0.683 ± 0.021 was obtained between loose smut and covered smut infection. Smut infected plants tended to be more susceptible to infection by stem rust than non-smutted plants.

Coffman, Stanton, Bayles, Wiebe, Smith and Tapke (3) studied the inheritance of resistance to *U. levis* in crosses between the resistant Markton and six susceptible varieties, namely, Early Champion, Ligowa, Scottish Chief, Swedish Select, Iogren and Aurora. In the crosses Markton x Early Champion, Markton x Ligowa and Markton x Swedish Select, approximately three-fourths of the progeny from the F_2 were infected and one-fourth were smut free,

indicating a single factor difference for resistance. In the crosses Markton x Scottish Chief, Iogren x Markton and Aurora x Markton, almost equal numbers of smut-free and of infected progeny lines from the F_2 plants were observed. Gradations of infection percentages were so complete that genetic classes seemed impracticable. Transgressive segregation for smut infection was observed.

Little or no correlation was found to exist between smut reaction and the following characters: panicle length, kernel length, kernel width, presence of awns, prominence of nerves in lemmas, and lemma color.

Experimental results.

As has already been stated, the F_3 was tested for reaction to covered smut in both 1931 and 1932. In the present analyses only the 1932 test will be considered as far greater infections were obtained in that year. The correlation coefficient for smut infection in 1931 and smut infection in 1932 was $+0.823 \pm 0.021$ in the Black Mesdag x Victory cross and $+0.601 \pm 0.739$ in the Black Mesdag x Banner cross.

The necessity for three sowings from F_2 seeds considerably reduced the number of plants in some F_3 families in the 1932 smut test. Only families with sufficient population to give a reliable indication of

inherent reaction are included in the following analyses. The standard set for the zero-infection class was as follows: no infection in 1931 (based on 40-50 plants), no infection in 1932 row of 20 or more plants. The standard for the intermediate infection class was a test of 20 or more plants. The minimum standard for inclusion of a family in the susceptible class is represented by a family which showed a comparatively very high infection in 1931, and 13 out of 17 plants infected in 1932. In a great majority of the cases the population of 1932 F_3 families ranged from 35 to 50 plants.

The classification of F_3 plants for smut reaction on the basis of percentage smut infection of F_3 families, together with parental reactions, is presented in Table II.

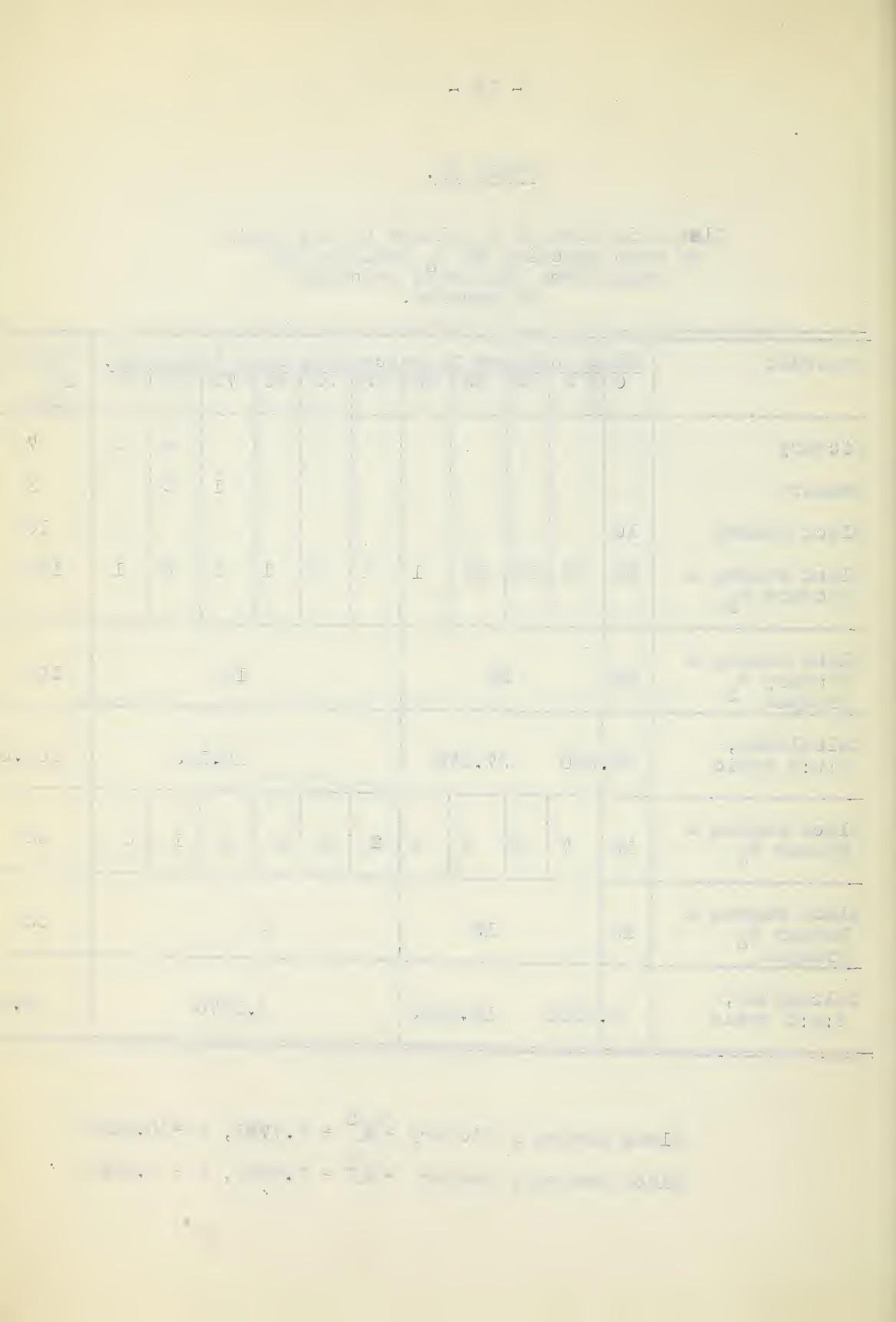
Table II.

Classification of F_2 plants on the basis
of smut reaction of F_3 families and
comparison with smut reaction
of parents.

Material	Class centers in percentage smut infection.											Number of plots
	0	5	15	25	35	45	55	65	75	85	95	
Victory										4	3	7
Banner									1	2		3
Black Mesdag	10											10
Black Mesdag x Victory F_3	28	23	16	18	1	1	2	1	6	5	1	102
Black Mesdag x Victory F_3 grouped	28		58						16			102
Calculated, 4:9:3 ratio	25.500		57.375						19.125			102,000
Black Mesdag x Banner F_3	15	7	3	3	2	2	0	0	0	1	0	33
Black Mesdag x Banner F_3 grouped	15		15						3			33
Calculated, 4:9:3 ratio	8.2500		18.5625						6.1875			33,0000

$$\text{Black Mesdag x Victory} = \chi^2 = 0.7721, P \Rightarrow 0.6065$$

$$\text{Black Mesdag x Banner} = \chi^2 = 7.8492, P = 0.0201$$



The results of the studies, particularly in the case of the Black Mesdag x Victory cross, could be explained, tentatively, by assuming the following factorial interactions:

Black Mesdag, RRPP

Banner or Victory, rrpp

R is a dominant factor for smut resistance which in a homozygous condition gives immunity. P is a supplementary factor for resistance which is less potent than R, and in a homozygous condition gives only partial resistance. The recessive allelomorphs r and p condition smut susceptibility.

Thus, the factorial interaction, with respect to smut reaction, in the present crosses may be represented as follows:

RRPP x rrpp

F_1	RrPp	Smut reaction based on F_3		
F_2		0 percent infection		
1 RRPP		0	"	"
2 RRpp		0.5-34.9	"	"
2 RrPP		0.5-34.9	"	"
4 RrPp		0.5-34.9	"	"
1 RRpp		0	"	"
2 Rrpp		0.5-34.9	"	"
1 rrPP		0.5-34.9	"	"
2 rrPp		35.0-100	"	"
1 rrpp		35.0-100	"	"

Detailed description: The pedigree diagram illustrates the inheritance of smut resistance. The F1 generation is RrPp. The F2 generation shows four distinct groups based on smut infection levels: 1) 0% infection (RRPP, RRpp, RrPP, RrPp), 2) 0.5-34.9% infection (2 RRpp, 2 RrPP, 4 RrPp), and 3) 35.0-100% infection (1 rrPP, 2 rrPp, 1 rrpp). The F3 generation is represented by triangles: Group 1 (0%) has three triangles, Group 2 (0.5-34.9%) has two triangles, and Group 3 (35.0-100%) has one triangle. This indicates that the 0% infection group is fully resistant (immunity), the 0.5-34.9% group shows partial resistance, and the 35.0-100% group is susceptible (infection).

Garber et. al. (12,13) in order to explain transgressive segregation for susceptibility in a Gopher x Black Mesdag cross, gave the following genotypes to the parents:

Black Mesdag, RRii

Gopher, rrII

(see historical review)

Except for a narrower range of infection (0 to 67.5 percent) their data on smut reaction of F_3 families agree with the data of the present experiment. Factorial analyses of both investigations will agree if the following parental genotypes be assumed:

Black Mesdag, RRPPii

Victory and Banner, rrppii

Gopher, rrPPII

The two-factor ratio assumed in each analysis will still hold good. This addition of factors PP to the genotype of Gopher accounts for the smaller degree of infection obtained in the cross involving that variety.

As dehulled seeds were used in the present investigation, the fact that Garber et.al. used hulled seed must be considered when comparing, directly, the infection ranges of the respective cultures. Garber et.al. reported an average smut infection of 19.5 percent for the eleven Gopher parental plots grown with the F_3 families. Under the conditions of the present investigation, the average infections obtained for four plots of Gopher were, when

hulled seed was used 1.6, and when dehulled seed was used 23.5 percent. It would appear, therefore, that conditions under which Garber et.al. grew their material were such that their infections from hulled seeds are closely comparable to infections obtained from dehulled seeds under the condition of the present investigation. The direct comparison of infection ranges made above is therefore, to a considerable extent, justifiable.

It should also be mentioned that Garber et.al. used as inoculum a mixture of the two oat smuts, while in the present study only covered smut was used.

The F_4 was not grown, except for the growing and testing for smut reaction of certain selections of agronomically desirable types from highly resistant or immune F_3 families. As the object of growing these lines was a purely economic one, no genetic analysis has been made. It might be stated, however, that all families showing immunity to smut in the F_3 were also immune in the F_4 , a behavior to be expected on the basis of the hypothesis.

INHERITANCE OF LEMMA COLOR

Historical review

A study of the literature dealing with the inheritance of lemma color in oats reveals an apparent difference in the genetical constitution of certain black-grained varieties (see Appendix). The recent work of Robb (31) brings out this point with particular clearness.

Reports on the inheritance of lemma color in crosses in which Black Mesdag was the black parent do not agree as to the number of factors involved. Garber and Quisenberry (11) found lemma color to be controlled by one factor in a cross between Black Mesdag and Gopher (white). Lunden (20) and Hayes, Griffey and Lunden (16) obtained similar results in crosses between Black Mesdag and homozygous strains from Minota x White Russian and White Russian x Victory crosses. Robb (31) observed a two-factor interaction in the cross Breseler's Prolific (white) x Black Mesdag. This difference in results may be explained in a number of ways: the white-grained parents may have carried, in the cases where only one factor was indicated, a factor inhibiting the expression of the factor for grey lemma color present in Black Mesdag; the parent designated as Black Mesdag may not have been the same; the environmental conditions, under which the experiments were conducted, that indicated one

factor for lemma color, ^{were conducted} may have been such that the factor for grey lemma color was not expressed.

Experimental results.

The lemma color of the F_1 grains of both crosses was similar to that of Black Mesdag. In the F_2 segregation occurred in both crosses for black, grey and white in approximately the ratio of 12:3:1. The F_2 data, together with tests of goodness of fit to the 12:3:1 ratio are given in Tables III and IV.

Table III.

F_2 segregation for lemma color in Black Mesdag x Victory and the test of goodness of fit to a 12:3:1 ratio.

Phenotype	Observed O	Calculated C	$O - C$	$(O-C)^2$	$\frac{(O-C)^2}{C}$
black	90	96.0	- 6.0	36.000	0.375
grey	31	24.0	+ 7.0	49.000	2.042
white	7	8.0	- 1.0	1.000	0.125
	128	128.0	0.0	$\chi^2 = 2.542$ $P = 0.2894$	

Table IV.

F_2 segregation for lemma color in Black Mesdag x
Banner and the test of goodness of
fit to a 12:3:1 ratio.

Phenotype	o	c	$o - c$	$(o-c)^2$	$\frac{(o-c)^2}{c}$
black	30	28.500	+ 1.500	2.250	0.079
grey	7	7.125	- 0.125	0.016	0.002
white	1	3.375	- 1.375	1.891	0.796
	38	38.000	0.000	$\chi^2 = 0.877$	
				$P = > 0.6065$	

The fit of the observed to the calculated data is good in the case of Black Mesdag x Victory and excellent in the case of Black Mesdag x Banner. It may be concluded from the P values obtained that the genetic ratio assumed is the correct one.

The F_3 data gives good substantiation of the F_2 hypothesis. However, since difficulty was encountered in distinguishing between white and grey colors, it was impossible to classify the different types of segregation in many instances. In Tables V and VI certain groupings are made in an attempt to overcome this difficulty.

TABLE V.

F_3 Segregation for lemma color in Black Mesdag
 \times Victory and test of goodness of fit
to a corrected 4:8:3:1 ratio.*

F_3 Behavior	o	c	$o - c$	$(o - c)^2$	$\frac{(o - c)^2}{c}$
homo. black	30	30.0	0.0	0.0	0.0
heter. black	60	60.0	0.0	0.0	0.0
homo. and heter. grey	31	31.0	0.0	0.0	0.0
homo. white	7	7.0	0.0	0.0	0.0
	128	128.0	0.0	$\chi^2 = 0.000$	
				P = > 0.8013	

* This is the F_3 ratio of the various types of segregation (With certain groupings) expected from a 12:3:1 F_2 ratio. It is corrected on the basis of actual numbers obtained in the F_2 .

1. $\frac{d}{dx} \sin x = \cos x$
2. $\frac{d}{dx} \cos x = -\sin x$
3. $\frac{d}{dx} \tan x = \sec^2 x$
4. $\frac{d}{dx} \sec x = \sec x \tan x$
5. $\frac{d}{dx} \csc x = -\csc x \cot x$
6. $\frac{d}{dx} \cot x = \operatorname{cosec}^2 x$

Table VI.

F_3 Segregation for lemma color in Black Mesdag
x Banner and test of goodness of fit
to a corrected 4:8:3:1 ratio.*

F_3 Behavior	o	c	$o - c$	$(o-c)^2$	$\frac{(o-c)^2}{c}$
homo. black	11	10.0	+ 1.0	1.0	0.100
heter. black	19	20.0	- 1.0	1.0	0.050
homo. and heter. grey	7	7.0	0.0	0.0	0.000
homo. white	1	1.0	0.0	0.0	0.000
	38	38.0	0.0	$\chi^2 = 0.150$	$P \rightarrow 0.8013$

* This is the F_3 ratio of the various types of segregation (with certain groupings) expected from a 12:3:1 ratio. It is corrected on the basis of actual numbers obtained in the F_2 .

The observed data are, in the case of both crosses, exceedingly close to the expected data based on the F_2 hypothesis.

These results are in agreement with those reported by Robb (31).

There is some indication of an accumulative effect of the factor for black and also of the factor for grey; but variations in color due to environmental conditions make it impossible to definitely establish the fact.

INHERITANCE OF AWN DEVELOPMENT

Historical review

The inheritance of awn development has been studied in a number of investigations, mainly in connection with interspecific crosses (See Appendix). The inheritance of the weak awn was studied by Love and Fraser (19) in the crosses Avena sterilis var. Burt x A. sativa var. Sixty Day and Red Texas x Burt. A single factor for awns was indicated. Fraser (8) later made a more intensive study of the genetics of the weak awn in crosses between Burt and Sixty Day. The expression of the weak awn was found to be controlled by a single factor. Surface (33), Love and Fraser (19), Fedorova (6) and others have found the strong awn to be strongly linked with the factor for wild type articulation in crosses between A. fatua and A. sativa. Segregation for awns occurred in the ratio of 1 sativa type : 2 intermediate types : 1 fatua type.

The mode of inheritance of the strong awn in crosses between varieties of A. sativa has not been established. Lunden (20) studied the inheritance of the strong awn in crosses between Black Mesdag and three purified hybrid lines from crosses between Victory or Minota and White Russian. No classification seemed possible because of nearly complete gradations between parental extremes.

The data, however, indicated the presence of one main factor for geniculate awns, with other factors probably concerned. Quisenberry (22) found, in a cross between A. sativa var. Victor (strong-awned) and A. sativa orientalis var. Sparrowbill (weak-awned, nearly awnless), that inheritance of awns was controlled by more than one genetic factor. Hayes, Griffee, Stevenson and Lunden (16) state, in regard to the inheritance of awns in a cross, (Minota x White Russian) x Black Mesdag, that "Without doubt several genetic factors are involved". They also state that awn development is probably greatly influenced by environmental conditions.

Experimental results.

When the study of the inheritance of awn development was commenced, it was assumed that the character was dependent upon several genetic factors, and that it was greatly influenced by environmental conditions; accordingly, great care was exercised in classifying F_2 and F_3 material. Every plant in both generations was described, with respect to awn development, as follows:

- (a) range of awn development (9 classes were used)
- (b) modal awn class
- (c) percentage of awned spikelets (10 classes estimated by inspection).

Genetic analyses were attempted, first, on the basis of the strongest awn expression (i.e., the upper extreme of the range), and second, on the basis of indices of number of awns (based on percentage of awned spikelets per plant). The former basis proved to be the most satisfactory, and it is believed that the data compiled by that method justifies the stating of a scheme of inheritance for awn development (See Plate II).

The F_2 data, corrected on the basis of F_3 behavior, are given in Tables VII and VIII.

TABLE VII.

F_2 Segregation for awn development in Black Mesdag x Victory and test of goodness of fit to the 12:3:1 ratio.

Phenotype	o	c	$o - c$	$(o - c)^2$	$\frac{(o - c)^2}{c}$
geniculate	98	96.0	+ 2.00	4.000	0.042
twisted	21	24.0	- 3.00	9.000	0.375
straight	9	8.0	+ 1.00	1.000	0.125
	128	128.0	0.00	$\chi^2 = 0.542$ $P = > 0.6065$	

$\frac{2\pi}{3}$	$(a - \varepsilon)$	$a = 0$	$a > 0$
\star	\star	\star	\star
\star	\star	\star	\star
\star	\star	\star	\star
\star	\star	\star	\star

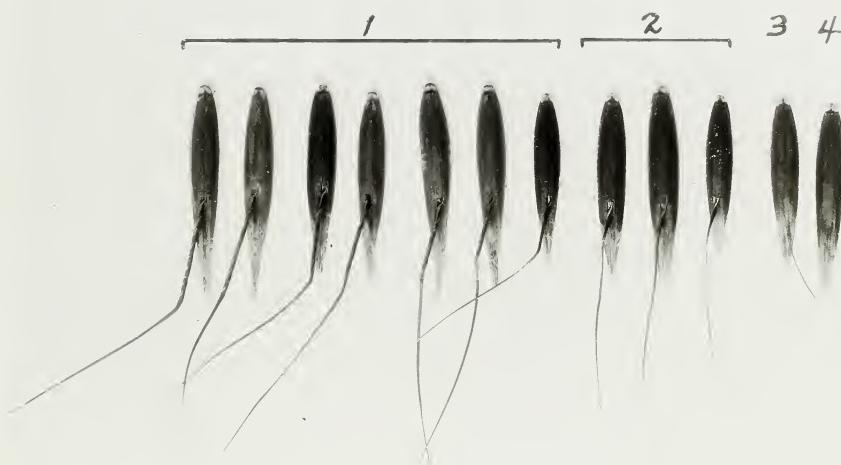


Plate II.

AWN CLASSES.

1. Strong, geniculate.
2. Twisted, non-geniculate.
3. Straight, non-twisted.
4. Absent.

TABLE VIII.

F_2 Segregation for awn development in Black
Mesdag x Banner and test of goodness
of fit to the 12:3:1 ratio.

Phenotype	o	c	$o - c$	$(o - c)^2$	$\frac{(o - c)^2}{c}$
geniculate	29	28,500	+ 0.500	0.250	0.009
twisted	6	7.125	- 1.125	1.266	0.178
straight	3	2.375	+ 0.625	0.391	0.165

$$\chi^2 = 0.352$$
$$P = > 0.6065$$

In both crosses the fit indicated is excellent.

The F_2 results may be explained by assuming the following factorial interactions:

Black Mesdag, SStt.

Victory or Banner, ssTT.

S is a dominant factor for strong, geniculate awns, T is a factor for twisted, non-geniculate awns. The double recessive will condition a few weak or no awns.

SStt x ssTT

F ₁	SsTt	
F ₂		F ₃ behavior.
12 strong, geniculate (S)	1 SStT	homo. S
	2 SsTT	seg. 3S : 1T
	2 SSTt	homo. S
	4 SsTt	seg. 12S:3T:1st.
	1 SStt	homo. S
	2 Sstt	seg. 3S: 1st
3 twisted, non-geniculate (T)	1 ssTT	homo. T
	2 ssTt	seg. 3T : 1 st
1 straight, non-twisted (st)	1 sstt	homo. st

The existence of awnless and nearly awnless hybrids indicates the possibility of a third genetic factor which operates in the absence of S and T, thus changing the ratio from 12:3:1 to 48:12:3:1. Of course, these types may be only variations due to the environment.

The F₃ data does not give a conclusive substantiation of the F₂ hypothesis. It is believed that the influence of environmental factors accounts for the lack of close correspondence between the two generations. Tables IX and X present the F₃ data classified according to the expected ratio based on the F₂ hypothesis.

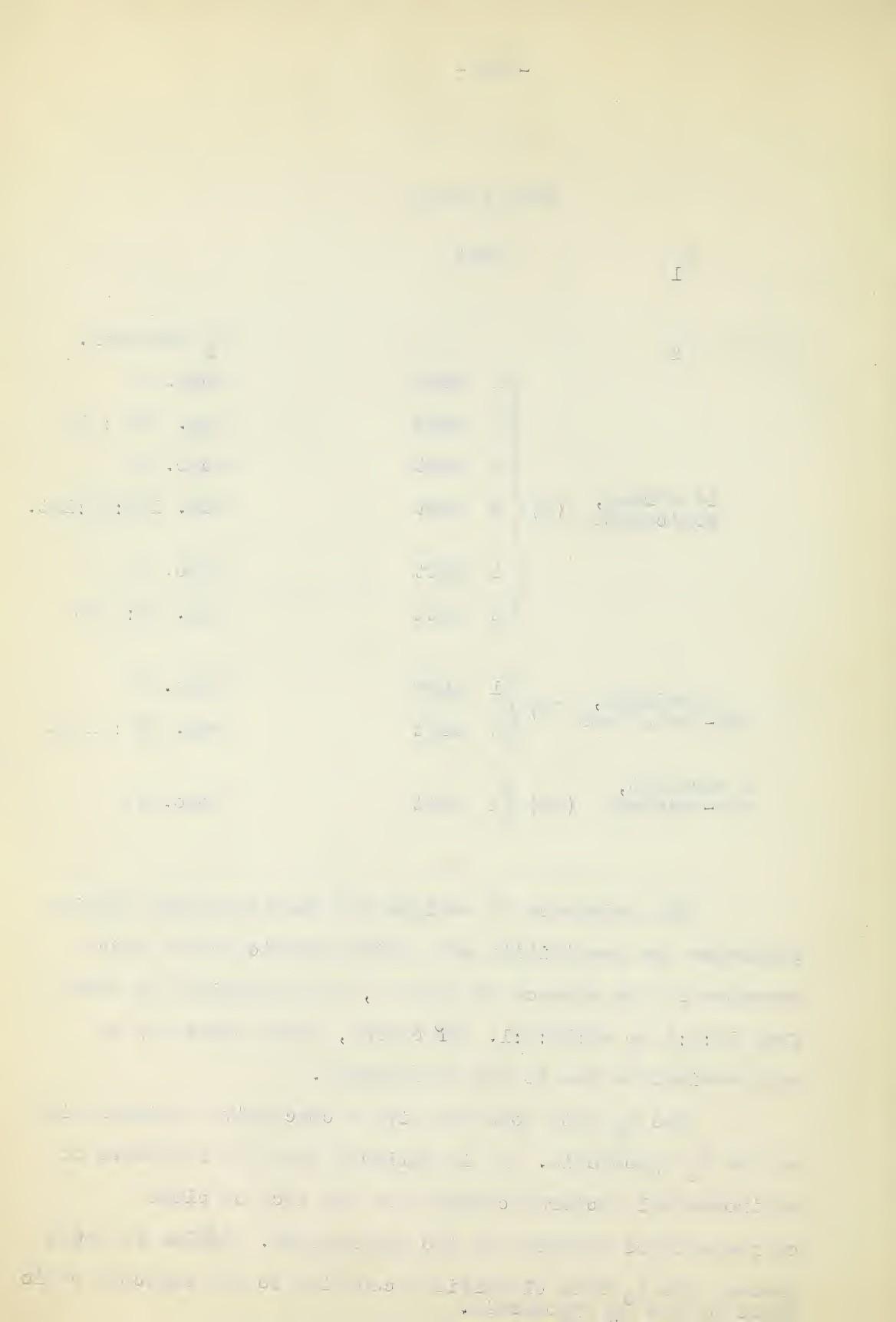


TABLE IX.

F_3 Segregation for awn development in Black Mesdag
 x Victory and test of goodness of fit to a
 corrected 4:4:2:2:1:2:1 ratio.*

F_3 behavior	o	c	o - c	$(o-c)^2$	$\frac{(o-c)^2}{c}$
homo. S	19	32.67	-13.67	186.869	5.720
12S : 3T : 1st	43	32.67	+10.33	106.709	3.266
3S : 1T	16	16.33	-0.33	0.108	0.066
3S : 1st	20	16.33	+3.67	13.469	0.825
homo. T	2	7.00	-5.00	25.000	3.571
3T : 1st	19	14.00	+5.00	25.000	1.786
homo. st.	9	9.00	0.00	0.000	0.000
	128	128.00	0.00		$\chi^2 = 15.234$ P = 0.0187

* This is the F_3 ratio of the various types of segregation expected from a 12:3:1 F_2 ratio. It is corrected on the basis of actual numbers obtained in the F_2 .

$\frac{\partial \lambda}{\partial u}$	$u \rightarrow 0$	$u \rightarrow \infty$	$u \rightarrow -\infty$
$\nabla \cdot \mathbf{F}$	$\nabla \cdot \mathbf{F} = 0$	$\nabla \cdot \mathbf{F} = 0$	$\nabla \cdot \mathbf{F} = 0$
$\nabla \times \mathbf{F}$	$\nabla \times \mathbf{F} = 0$	$\nabla \times \mathbf{F} = 0$	$\nabla \times \mathbf{F} = 0$
$\nabla \cdot \mathbf{E}$	$\nabla \cdot \mathbf{E} = 0$	$\nabla \cdot \mathbf{E} = 0$	$\nabla \cdot \mathbf{E} = 0$
$\nabla \times \mathbf{E}$	$\nabla \times \mathbf{E} = 0$	$\nabla \times \mathbf{E} = 0$	$\nabla \times \mathbf{E} = 0$
$\nabla \cdot \mathbf{B}$	$\nabla \cdot \mathbf{B} = 0$	$\nabla \cdot \mathbf{B} = 0$	$\nabla \cdot \mathbf{B} = 0$
$\nabla \times \mathbf{B}$	$\nabla \times \mathbf{B} = 0$	$\nabla \times \mathbf{B} = 0$	$\nabla \times \mathbf{B} = 0$

TABLE X.

F_3 Segregation for awn development in Black
Mesdag x Banner and test of goodness
of fit to a corrected
 $4:4:2:2:1:2:1$ ratio.*

F_3 behavior	o	c	$o - c$	$(o-c)^2$	$\frac{(o-c)^2}{c}$
homo. S	6	9.667	-3.667	13.447	1.391
12S : 3T : 1st	15	9.667	+5.333	28.441	2.942
3S : 1T	0	4.833	-4.833	23.358	4.833
3S : 1st	8	4.833	+3.167	10.030	2.075
homo. T	0	2.000	-2.000	4.000	2.000
3T : 1st	6	4.000	+2.000	4.000	1.000
homo. st	3	3.000	0.000	0.000	0.000
	38	38.000		$\chi^2 = 14.241$	$P = 0.0274$

* This is the F_3 ratio of the various types of segregation expected from a $12:3:1$ F_2 ratio. It is corrected on the basis of actual numbers obtained in the F_2 .

A poor fit is indicated by the χ^2 test in both tables. It will be noticed that frequencies are low in homozygous classes other than the recessive class. This is to be expected where external factors exert strong influence on genetic material. It seems fair to assume that many genotypically homozygous types, whose expressions are modified by the environment, would therefore, appear to be segregating.

$\Delta \tau$	$\rho - \rho_0$	ρ	σ	σ_{min}
0	0	0	0	0
100	100	100	100	100
200	200	200	200	200
300	300	300	300	300
400	400	400	400	400
500	500	500	500	500
600	600	600	600	600
700	700	700	700	700
800	800	800	800	800
900	900	900	900	900
1000	1000	1000	1000	1000

$$\frac{\partial \psi}{\partial t} = 0$$

and the boundary condition is given by

$$\psi(0, t) = \psi(L, t) = 0 \quad \forall t \in [0, T]$$

where L is the total length of the domain.

The initial condition is given by

$$\psi(x, 0) = \psi_0(x) \quad \forall x \in [0, L]$$

where $\psi_0(x)$ is the initial profile of the function.

The numerical solution is obtained by discretizing the spatial domain and time interval.

The spatial domain is discretized into N points, and the time interval is discretized into M points.

The spatial points are denoted by x_i , where $i = 1, 2, \dots, N$.

INHERITANCE OF RACHILLA PUBESCENCE.

Historical review

The inheritance of rachilla pubescence has not been extensively investigated (See Appendix). In crosses between Avena fatua and A. sativa, Surface (33) and Fedorova (6) found rachilla pubescence to be linked with the factor for fatua type articulation, segregation for pubescence occurring in the ratio of 1 sativa type : 2 intermediate types : 1 fatua type. Lunden (20) reported that pubescence of the rachilla is controlled by a single factor. The F_1 generation was intermediate. Hayes, Griffee, Stevenson and Lunden (16) in a study of the crosses, (White Russian x Victory) x Black Mesdag and (White Russian x Minota)X Black Mesdag, observed segregation in the ratio of 3 (few hairs) : 1 (many hairs). Odland (21), working with a cross between Early Gothland (A. sativa) and Garton 784 (A. sativa orientalis), found segregation for rachilla pubescence in the ratio of 3 smooth : 1 hairy.

Experimental results.

Two methods of studying the inheritance of rachilla pubescence were used throughout the present investigation: first, length of hairs and, second, number of hairs was used as the unit of inheritance. A strong, positive correlation exists between these two aspects of rachilla pubescence.

(See Table XVI). Both systems of classification were utilized in working out an inheritance scheme, though phenotypic classes are based, primarily, on length of hairs.

Originally, the F_2 data were classified on the basis of presence and absence of hairs. The data fitted the ratio 3 pubescent : 1 glabrous very well. When the F_3 was examined, however, it was found that most of the glabrous types produced hairs, indicating the presence of interclasses within the original recessive group. The F_2 material was then re-classified with great care; a magnifying glass was used to aid in the detection of the slightest indication of pubescence. Classification was based on six classes of pubescence as well as the glabrous class. It was found that there are, apparently, two phenotypic classes of pubescence, long hairs and short hairs; the long hairs were relatively abundant while the short hairs occurred in small numbers - often the inspection of several grains would disclose only a single hair.

Tables XI and XII summarize the F_2 data as corrected on the basis of F_3 behavior.

TABLE XI.

F₂ Segregation for rachilla pubescence in Black Mesdag x Victory and test of goodness of fit to the 12:3:1 ratio.

Phenotype	o	c	o - c	(o-c) ²	$\frac{(o-c)^2}{c}$
long	95	96.0	- 1.0	1.0	0.010
short	25	24.0	+ 1.0	1.0	0.042
absent	8	8.0	0.0	0.0	0.000
	28	28.0	0.0	$\chi^2 = 0.052$	
				P = >0.6065	

TABLE XII.

F₂ Segregation for rachilla pubescence in Black Mesdag x Banner and test of goodness of fit to the 12:3:1 ratio.

Phenotype	o	c	o - c	(o-c) ²	$\frac{(o-c)^2}{c}$
long	27	28.500	-1.500	2.250	0.079
short	9	7.125	+1.875	3.516	0.493
absent	2	2.375	-0.375	0.141	0.059
	38	38.000	0.000	$\chi^2 = 0.631$	
				P = >0.6065	

In both crosses the fit of the observed to the calculated data is very close.

The F_2 results may be explained by postulating the following hypothesis:

Black Mesdag , NNNF.

Banner or Victory, nnff.

N is a dominant factor which conditions numerous, fairly long hairs on the rachilla. F is a supplementary factor, hypostatic to N, which gives a few short hairs on the rachilla. The double recessive produces a glabrous condition.

NNFF x nnff.

F_1 NnFf

F_2		F_3 behavior.
12 numerous ,long (N)	1 NNFF 2 NnFF 2 NNff 4 NnFf	homo. N seg. 3N : 1F homo. N seg. 12N : 3F : 1nf
	1 NNff 2 Nnff	homo N seg. 3N : 1nf

3 few, short (F)	1 nnFF 2 nnFf	homo. F seg. 3F : 1 nf
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1 absent (nf)	1 nnff	homo. nf
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The expression of rachilla hairs in the F_3 was stronger than in the F_2 due to environmental influences. It was found that the environment affected the length more than it did the number of hairs: that is to say, that, while the short hair expression of the F_2 might be "stepped-up" to medium length in the F_3 , the number of hairs associated with short expression remained more or less constant in both generations. This fact was utilized in distinguishing F_3 phenotypes in terms of the F_2 expressions. The data thus compiled affords an excellent substantiation of the F_2 hypothesis.

TABLE XIII.

F_3 Segregation for rachilla pubescence in Black Mesdag x Victory and test of goodness of fit to a corrected 4:4:2:2:1:2:1 ratio.*

F_3 behavior	o	c	o-c	$(o-c)^2$	$\frac{(o-c)^2}{c}$
homo. N	34	31.67	+2.33	5.4289	0.1714
12N:3F:lnf	34	31.67	+2.33	5.4289	0.1714
3N : 1F	16	15.83	+0.17	0.0289	0.0018
3N : lnf	11	15.83	-4.83	23.3289	1.4737
homo. F	6	8.33	-2.33	5.4289	0.6517
3F : lnf	19	16.67	+2.33	5.4289	0.3257
homo. nf	8	8.00	0.00	0.0000	0.0000
	128	127.99			$\chi^2 = 2.7957$ $P = 0.8315$

* This is the F_3 ratio of the various types of segregation expected from a 12:3:1 F_2 ratio. It is corrected on the basis of actual numbers obtained in the F_2 .

TABLE XIV.

F₃ Segregation of rachilla pubescence in Black Mesdag x Banner and test of goodness of fit to a corrected 4:4:2:2:1:2:1 ratio.*

F ₃ behavior	o	c	o-c	(o-c) ²	$\frac{(o-c)^2}{c}$
homo. N	12	9.0	+3.0	9.00	1.0000
12N : 3F : lnf	8	9.0	-1.0	1.00	0.1111
3N ; 1 F	4	4.5	-0.5	0.25	0.0556
3N : 1 nf	3	4.5	-1.5	2.25	0.5000
homo. F	2	3.0	-1.0	1.00	0.3333
3F : lnf	7	6.0	+1.0	1.00	0.1667
homo. nf	2	2.0	0.0	0.00	0.0000
	38	38.0	0.0	$\chi^2 = 2.1667$	P = 0.9012

* This is the F₃ ratio of the various types of segregation expected from a 12:3:1 F₂ ratio. It is corrected on the basis of actual numbers obtained in the F₂.

The P values calculated in Tables XIII and XIV both indicate an excellent fit between observed and calculated ratios.

The F₃ breeding behavior of plants in the glabrous class of the re-classified F₂ indicated the presence of still another supplementary factor or other modifying condition. Among the eight plants classified as glabrous in the Black Mesdag x Victory cross, two bred true, while six segregated as follows for hairlessness and one or more very short hairs per plant, respectively: 34:4, 30:4, 31:6, 25:10, 16:13, 24:19.

In the first three cases the hairs were distinctly longer and more numerous than in the last three instances, where the hairs were very minute. Of the two plants classified as glabrous in the Black Mesdag x Banner cross, one bred true for hairlessness while the other produced 19 plants showing no hairs and 15 plants showing one or more very minute hairs.

STUDIES ON CORRELATED INHERITANCE.

Correlations between smut reaction and other characters.

The detection of linkage relationships between disease reaction and morphological characters is of economic significance because it gives an indication of the possibilities of combining desirable expressions of the latter with disease resistance by hybridization. When the mode of inheritance of the disease reaction in question is difficult to study by direct methods, correlations with characters of known inheritance provide the basis of an indirect method of attacking the problem.

Review of the literature on this topic was given in connection with the historical review of studies on the inheritance of smut reaction.

The formulae used in the present correlation studies are those given by Hayes and Garber (15, pp. 43-48).

In the studies of correlation between smut reaction and the various grain characters, the population was 102 for the Black Mesdag x Victory cross and 33 for the Black Mesdag x Banner cross. It is realized that the latter population is too small to give very reliable results; this is especially true where the correlation ratio was used.

A summary of the constants calculated are presented in Table XV.

In the Black Mesdag x Victory cross, significant correlations were obtained, by the correlation ratio method, between percentage smut infection and the following characters: strength of awns ($r = +0.323 \pm 0.060$), number of awns ($r = -0.312 \pm 0.060$), number of rachilla hairs ($r = -0.323 \pm 0.060$). The signs were determined by inspection of the correlation surfaces.

Though these correlation values are quite significant in the light of their respective probable errors, they are so small that it is questionable if actual significant correlation exists between the variables tested. The scatter of the data on the correlation surfaces does not indicate the existence of correlation; the correlation coefficients for the same surfaces indicate that there are no significant relationships between the variables in question (See Table XV). In order to explain the situation it will be necessary to examine the reliability of the correlation ratio as a measure of correlation.

The correlation ratio is based on the assumption that if no correlation exists in a given surface, the mean of each row (or column) $y\bar{X}$ will be equal to the mean of the entire distribution \bar{X} . Therefore, $y\bar{X} - \bar{X} = 0$. Completing the computation, $\sqrt{\sum [f(y\bar{X} - \bar{X})^2] / N} = 0$. This value is the numerator of the fraction which equals η . Therefore, $\eta = 0$. An increase in the association between the variables will produce a proportional increase in η by increasing the difference $y\bar{X} - \bar{X}$. It will be seen that if the frequency of each row is not large enough to give a reliable row mean the resulting value of η cannot be reliable. In a great many correlation surfaces, regardless of the total population of the distributions, the rows passing through the outer borders of the scatter have not sufficient numbers to give a reliable row mean. In the present study, it was found that it was these rows which gave most of the size to the summation $\sum [f(y\bar{X} - \bar{X})^2]$. While it is recognized that the extreme variants at the edge of the scatter have great influence on the value of the correlation constant computed by other methods, the fact remains that the correlation ratio method is not reliable, in many cases, for reasons stated.

The correlation ratio should be applied to non-linear distributions in which, irrespective of the total population, each row (or column) has a frequency large enough to give a reliable mean. The number of rows should be few in order that each row may have, if possible, a large frequency.

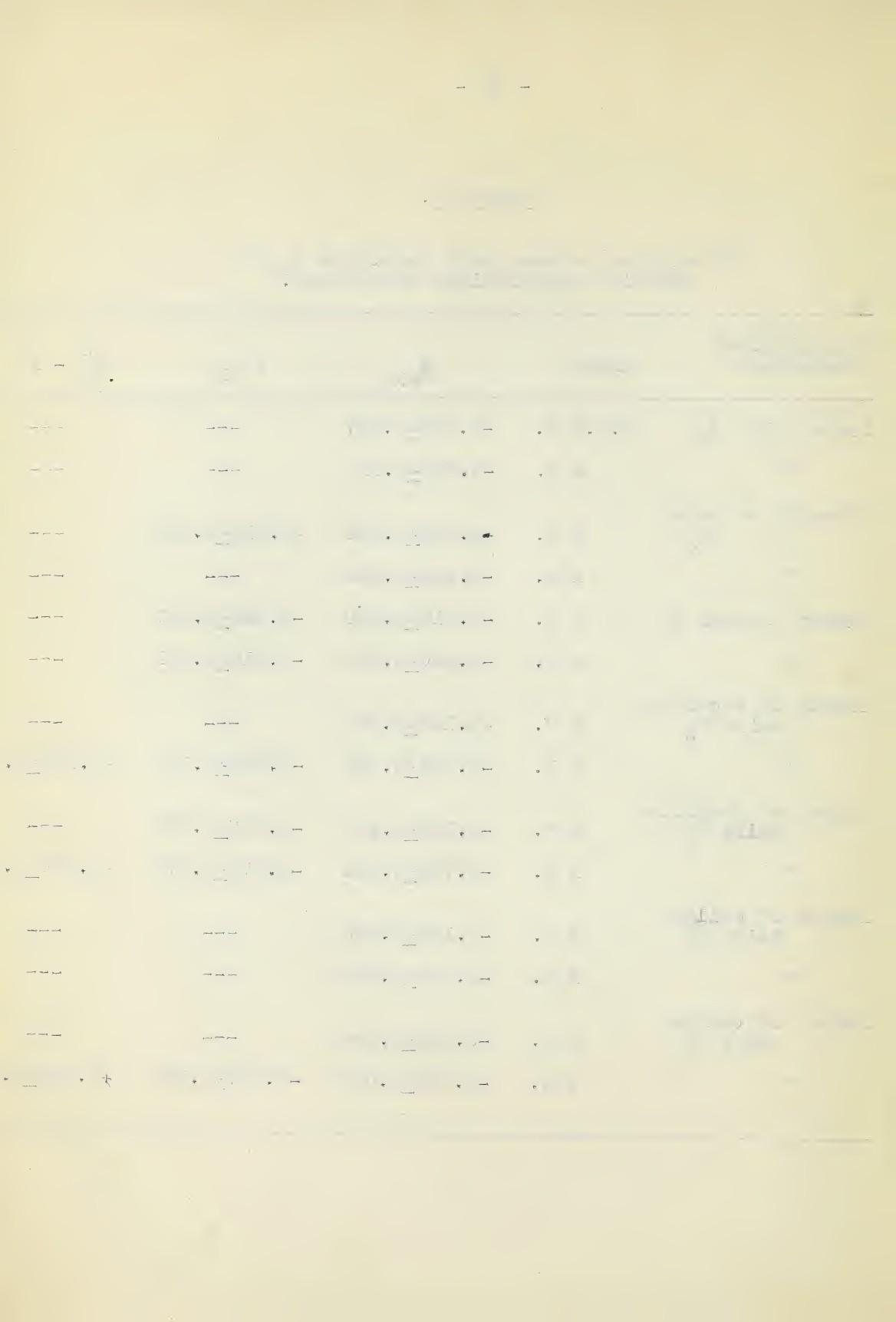
In the Black Mesdag x Banner cross, significant correlations were obtained, by the correlation ratio method, between percentage smut infection and the following characters: strength of awns (-0.455 ± 0.093), number of awns (-0.480 ± 0.090), length of rachilla hairs (-0.446 ± 0.095), number of rachilla hairs (-0.783 ± 0.046), length of callus hairs (-0.469 ± 0.092), number of callus hairs (-0.686 ± 0.062).

Owing to the small populations used in these computations, it is felt that no definite conclusions regarding linkages should be drawn where only the correlation ratio is significant. In the case of two characters, the correlation coefficient was also significant, namely, number of rachilla hairs (-0.578 ± 0.078) and number of callus hairs (-0.347 ± 0.103). In these cases, particularly in the former, it would seem that a loose association with smut ^{reaction} ~~infection~~ might be concluded.

TABLE XV.

Correlation between smut infection F_3 and certain morphological characters.

Morphological Characters	Cross	r_{xy}	r_{xy}	$r^2 - r^2$
lemma color F_2	B.M. x V.	-0.044+0.067	---	---
"	x B.	-0.230+0.111	---	---
Strength of awns F_3	x V.	+0.323+0.060	+0.010+0.067	---
"	x B.	-0.455+0.093	---	---
number of awns F_3	x V.	-0.312+0.060	-0.020+0.067	---
"	x B.	-0.480+0.090	-0.318+0.111	---
length of rachilla hairs F_3	x V.	+0.123+0.066	---	---
"	x B.	-0.446+0.095	-0.258+0.110	+0.132+0.075
number of rachilla hairs F_3	x V.	-0.323+0.060	-0.097+0.066	---
"	x B.	-0.783+0.046	-0.578+0.078	+0.280+0.104
length of callus hairs F_3	x V.	-0.129+0.085	---	---
"	x B.	-0.469+0.092	---	---
number of callus hairs F_3	x V.	-0.202+0.084	---	---
"	x B.	-0.686+0.062	-0.347+0.103	+0.530+0.099



Correlation between various grain characters.

Studies on the correlation existing between grain characters are of economic interest, for they indicate the possibilities of combining desirable expressions of the characters through hybridization. Such studies also contribute to genetical knowledge by disclosing the presence or absence of genetic linkages.

The formula for the coefficient of contingency used in the present study is that given by Hayes and Garber (15, pp. 49-50).

Using the coefficient of contingency method, significant correlations were obtained between the following characters:

Black Mesdag x Victory;

number of rachilla hairs and number of
callus hairs, $C_1 = +0.499 \pm 0.117$.

Black Mesdag x Banner,

number of rachilla hairs and strength
of awns, $C_1 = +0.553 \pm 0.152$.

number of rachilla hairs and number
of callus hairs, $C_1 = +0.575 \pm 0.147$.
number of callus hairs and strength of
awns, $C_1 = +0.645 \pm 0.128$.

There can be no doubt regarding the existence of correlation between the expressions of these characters. However, the presence of such correlations is not, necessarily definite indication of genetic linkages. It is probable that there is segregation for physiological characters in the present material. A set of physiological factors which promotes strong expression of, say, rachilla hairs, might be expected to produce a like expression of a similar character such as callus pubescence, regardless of genetic relationships. Environmental factors, such as the soil, may vary in such a way as to produce physiological differences among the plants, which in turn might result in a correlation between certain characters in a given plant.

When working with closely related characters, such as awn development, rachilla pubescence, and callus pubescence, in a hybrid population, multiple correlations should be calculated before drawing conclusions regarding the existence of genetic linkages.

TABLE XVI.

Correlations between the various grain characters.

Variables	Cross	C_1
number of rach.hairs F_3 and length of rach.hairs F_3	B.M. x V.	+0.775 \pm 0.048
number of rach.hairs F_3 and strength awns F_3 .	x B.	+0.553 \pm 0.152
number of rach.hairs F_3 and number callus hairs F_3	x V.	+0.499 \pm 0.117
number of rach.hairs F_3 and number of callus hairs F_3	x B.	+0.575 \pm 0.147
strength of awns F_3 and number of callus hairs F_3	x B.	+0.645 \pm 0.128

ECONOMIC SIGNIFICANCE.

The practical objective of the investigation - the production of constant hybrid strains possessing the desirable agronomic characters of the one parent and the smut resistance of the other - has been realized. One F_3 family from the Black Mesdag x Victory cross was, apparently, homozygous for white, plump grains, weak awns, strong straw, mid-season maturity and smut immunity. Forty-eight F_4 lines from this family were grown and all proved to be constant for the characters mentioned. These lines are probably equal to Victory in quality and equal to Black

Mesdag in smut resistance. Each line has been bulked and will be increased separately and tested for yield. Several hundred plant selections of weak-awned, white-grained segregates were made in other smut immune F_3 families. As the characters, white grain and weak awns, are recessive and the character, smut immunity, is homozygous dominant, the selections bred true for these characters in the F_4 . Many promising lines have been observed which will be increased for yield tests.

SUMMARY.

The F_2 and F_3 generations from the crosses Black Mesdag x Victory and Black Mesdag x Banner were studied for smut reaction, lemma color, awn development and rachilla pubescence. Black Mesdag has black grains, strong awns, pubescent rachillas and is immune ^{from} ~~to~~ smut infection. Victory and Banner have white grains, weak awns, glabrous ~~lemmas~~ rachillas and are susceptible to smut infection. Results of the various phases of the investigation are as follows:

1. Reaction to covered smut was studied in the F_3 generations. The lemma and palea were removed from the seed prior to inoculation with smut spores. Segregation for smut reaction occurred in the ratio, 4 immune : 9 moderately resistant : 3 susceptible. Hybrid susceptibility was as high as 95% and coincided with the susceptibility of the non-resistant parent. Immune F_3 lines bred true for immunity in the F_4 . It is concluded that a two-factor

difference for smut reaction exists between the parents.

2. Segregation in the F_2 for lemma color occurred in the ratio of 12 black : 3 grey : 1 white. The F_3 data gave a close substantiation to this ratio.

3. Segregation in the F_2 for awn development occurred in the ratio of 12 strong , geniculate : 3 twisted, non-geniculate : 1 straight, non-twisted. The F_3 data did not show a close correspondence to the expected data owing to environmental influences.

4. Segregation in the F_2 for rachilla pubescence occurred in the ratio of 12 numerous , long hairs : 3 few, short hairs : 1 glabrous. The F_3 data gave a close substantiation to the F_2 ratio. Some evidence of an additional factor for pubescence was observed.

5. No significant correlation between smut reaction and the various grain characters studied was found in the case of the Black Mesdag x Victory cross. A moderate degree of association between smut infection and the glabrous condition of the rachilla and of the callus was found in the Black Mesdag x Banner cross.

6. A moderate degree of association was found to exist between rachilla pubescence and awn development in both crosses. In the Black Mesdag x Banner cross a moderate degree of association existed, also, between rachilla pubescence and callus pubescence, and between callus pubescence and awn development. As segregation for physiological factors might account for these associations, no definite

conclusions are drawn regarding genetic linkages.

7. Homozygous strains, possessing white grains, weak awns and other desirable agronomic characters in combination with smut immunity, were selected for further testing.

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APPENDIX.

Tabular summary of results of studies by a number of investigators on the inheritance of certain grain characters.

Investigators	Material	Lemma color	Awn development	Rachilla pubescence
Nilsson-Ehle, 1909- 14. Quoted by Surface (33).		48 black : 12 grey : 3 yellow : 1 white	Much effected by environment. Wide variation in pure lines. Negative correlation with yellow lemma	
Zade, 1912 Quoted by Love and Craig (18)	<u>Avena fatua</u> x <u>A. sativa</u> .		1 <u>sativa</u> : 2 intermediate : 1 <u>fatua</u> *	
Surface, 1916 (33)	<u>A. fatua</u> x <u>A. sativa</u> var. Kher- son	12 black : 3 grey : 1 yellow	1 <u>sativa</u> : 2 intermediate : 1 <u>fatua</u> . Linked with artic- ulation	1 <u>sativa</u> : 2 intermediate : 1 <u>fatua</u> . Linked with artic- ulation
Gaines, 1917 (9)	F ₂ of 10 crosses between 6 white and 3 black var- ieties	3 black : 1 white		
Love and Fraser, 1917 (19)	<u>A. fatua</u> x <u>A. sativa</u> var. Sixty- Day and other crosses		1 awnless : 2 part- ially awned : 1 fully awned	
Love and Craig, 1918 (18)	<u>A. fatua</u> x <u>A. sativa</u> var. Sixty- Day	12 black : 3 grey : 1 white	Gene for yellow lemma color inhibits awns in some var- ieties	
Fraser, 1919 (8)	<u>A. sterilis</u> var. Burt x <u>A. sativa</u> var. Sixty-Day	48 red : 15 yellow : 1 white	1 awnless : 2 part- ially awned : 1 fully awned, or 3 partially awned : 1 fully awned	
Lunden, 1925 (20)	F ₁ and F ₂ of cross- es between Black Mesdag and purifi- ed white hybrid lines	3 black : 1 white	One main factor producing genicul- ate awns. Probably supplementary factors for very strong awns	Controlled by single factor F ₁ intermediate

Appendix (Continued).

Investigator	Material	Lemma color	Awn development	Rachilla pubescence
Quisenberry, 1926 (22)	F and F ₃ of cross between <u>A. sativa</u> and <u>A. sativa orientalis</u>	3 black : 1 white	More than one genetic factor indicated	
Hayes et.al. 1928 (16)	Crosses between Black Mesdag and purified white hybrid lines	3 black : 1 white	Several factors involved. Much influence by environment	3 few hairs: 1 many hairs
Garber and Quisenberry, 1928 (11)	Gopher x Black Mesdag	3 black : 1 white		
Odland, 1928 (21)	<u>A. sativa</u> x <u>A. sativa orientalis</u>	3 black : 1 white		3 glabrous : 1 pubescent
Tschermak, 1929 quoted by Florell (7)	<u>A. sativa</u> x <u>A. fatua</u>		Complete linkage "wild" articulation and "wild" awn development	
Fedorova, 1930 (6)	<u>A. sativa</u> x <u>A. fatua</u>	9 black : 3 brown : 3 grey : 1 yellow	1 <u>sativa</u> : 2 intermediate : 1 <u>fatua</u> . Linked with articula-	1 <u>sativa</u> : 2 intermediate : 1 <u>fatua</u> Linked with articulation
Florrel, 1931 (7)	<u>A. fatua</u> x <u>A. sterilis ludoviciana</u>	3 brown (<u>fatua</u>): 1 grey-white (<u>ludoviciana</u>)		
	<u>A. fatua</u> x <u>A. byzantina</u> var. Fulghum		Almost complete linkage between <u>fatua</u> awning and <u>fatua</u> articulation. 1-factor	
	<u>A. sterilis ludoviciana</u> x <u>A. sativa</u> var. North Finnish		Complete linkage between <u>sterilis</u> awning and <u>sterilis</u> articulation. 1-factor	
	<u>A. sterilis ludoviciana</u> x <u>A. sativa</u> var. Probateier		ditto.	
	<u>A. sterilis macrocarpa</u> x <u>A. sativa</u> var. Richland		ditto.	

Appendix (Continued)

Investigator	Material	Lemma color	Awn development	Rachilla pubescence
Welsh, 1931 (35)	Heigira strain x Banner	1 white : 2 seg.: 1 yellow		
	Richland x purified white hybrid strain	1 white : 2 white- yellow : 1 yellow		
	Joanette strain x purified white hybrid strain	12 black : 3 grey : 1 white		
	Heigira Strain x Monarch Strain	12 black : 3 white : 1 yellow		
Robb, 1932 (31)	F ₂ of 6 crosses between 4 black and 3 white varieties	3 black : 1 white		
	F ₂ of crosses be- tween 2 black (incl. Black Mes- dag) and 2 white varieties	12 black : 3 grey : 1 white		
	F ₂ of 16 crosses between 1 black (Orion) and 9 white varieties	60 black : 3 grey : 1 white		

* The term fatua refers, with respect to awn development, to a condition similar to that found in A. fatua, namely, strong geniculate awns on all grains of the spikelet. The term sativa refers to a condition of awn development similar to that of the variety of A. sativa used in the cross in question.



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